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The western and southern distribution of *Mesocyclops edax* (S. A. Forbes) (Crustacea: Copepoda: Cyclopoida)

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Abstract.—A review of published records and material of the cyclopoid copepod *Mesocyclops edax* (S. A. Forbes) established its presence in the drainage basins of the Colorado and Columbia Rivers in the western U.S.A., and verified published records from Cuba, Guatemala, and Mexico. *Mesocyclops nicaraguensis* Herbst is a junior synonym of *M. edax.* We provide supplementary morphological observations and describe certain morphological variations observed in some populations of *M. edax.*

The cyclopoid copepod *Mesocyclops edax* (S. A. Forbes, 1891) is a common and often numerous plankter in surface waterbodies of North America, and its biology and genetics have been the subject of many reports (e.g., Williamson 1986; Wyngaard 1991; Wyngaard et al. 1985, 1995). *Mesocyclops edax* is widespread in south-central and eastern Canada (Patalas 1986) and in the conterminous U.S.A. east of the Rocky Mountains; the animals undergo diapause in winter in colder latitudes. The western and southern limits of *M. edax* are less well documented. Patalas (1986) failed to find it in his own collections or in published records west of the Canadian Pacific continental divide. Published records of *M. edax* from the western U.S.A. are few, and confirmed records from Mexico and Central America even fewer. We review western and southern records of *M. edax,* confirming those records where possible through examination of available specimens.

The question of the synonymy of *Mesocyclops nicaraguensis* Herbst, 1960 with *M. edax,* first raised by Cole (1976), has continued unresolved. We compared specimens from the type-locality of *M. nicaraguensis* in Lake Nicaragua, and from other waterbodies in Nicaragua to populations of *M. edax* from across North America.

Dussart (1985) and Dahms & Fernando (1995a) redescribed adult *M. edax.* We add observations on certain morphological features of interest for the systematics of the genus, and note some morphological variations observed during the course of this study.

Specimens were deposited in the collections of the National Museum of Natural History (USNM), and the Centro para la Investigación en Recursos Acuáticos de Nicaragua, Universidad Nacional Autónoma de Nicaragua (CIRA/UNAN).

Order Cyclopoida G. O. Sars, 1886
Family Cyclopidae Burmeister, 1834
Subfamily Cyclopinae Dana, 1853
Genus *Mesocyclops* G. O. Sars, 1914
Mesocyclops edax (S. A. Forbes, 1891)
Figs. 1–3

Cyclops edax S. A. Forbes, 1891:709–710, 715, 717, 718, pl. III fig. 15, pl. IV figs. 16–19.

Cyclops leuckarti Claus, 1857 (partim).—Marsh 1893:191, 193, 209–211, 224, pl. IV fig. 17, pl. V figs. 2–6.

Mesocyclops edax.—G. O. Sars 1914:58.
Cyclops leuckharti.—Coker 1926:230–234, 247–248, 257, pl. 40 figs. 5–7.
Mesocyclops Leuckarti edax.—Kiefer 1929a:306–307, figs. 4, 5.
Mesocyclops obsoletus (Koch, 1838).—C. B. Wilson 1929:129.
Mesocyclops nicaraguensis Herbst, 1960: 27, 42–45, figs. 33–41.
Non *Cyclops simplex* Poggenpol, 1874.—Herrick, 1887:14, 17–18, pl. VII fig. 1.
?Non *Cyclops tenuissimus* Herrick, 1883: 499–500, pl. V figs. 24, 25, pl. VI, figs. 20, 21.

Material examined.—Canada: USNM 79773, 10 ♀♀, Lake-of-the-Woods, Ontario, 17 Jul 1909. USNM 251908, 6 ♀♀, 8 ♂♂, Red Bridge Pond, Halifax, Nova Scotia, 8 Jul 1992, leg. G. A. Wyngaard. U.S.A.: USNM Acc. No. 120079 (Marsh Collection), 1 ♀, slide, Hutchins, Texas, C. D. Marsh prep. no. 3101. USNM 62590, 10 ♀♀, Lake Erie, 12 Jul 1928, don. Buffalo Society of Natural Science. USNM 78730, 10 ♀♀, Welaka, Florida, 1 Apr 1938, leg. L. Cable. USNM 216873, 10 ♀♀, Crane's Pond, Newport, North Carolina, 24 Aug 1984, leg. M. C. Swift. USNM 235221, 7 ♀♀, Lake Powell, Utah, 17 Jan 1985, leg. L. Haury. USNM 251156, 60+ ♀♀ ♂♂ and copepodids, Lake Union, Seattle, State of Washington, 47°39′12″N, 122°19′24″W, 10 Oct 1991, leg. Parametrix Inc. for Municipality of Metropolitan Seattle (METRO), gift of J. R. Cordell. USNM 264309, 13 ♀♀, Hueco Spring I, near New Braunfels, Cornal Co., Texas, 8–10 Aug 1992, leg. C. B. Barr. USNM 278133, 1 ♀ 2 ♂♂ 2 copepodids, San Joaquin River, Fresno, California, 10 Sep 1995, leg. S. Callison. Mikropräparate 2993 and 2994, 1 ♀, partly dissected on 2 slides, Lake Otay, San Diego, California, 29 Feb 1936, leg. Light, prep. F. Kiefer, Kiefer Collection, Staatliches Museum für Naturkunde Karlsruhe. 20 ♀♀ ♂♂, culture, New Orleans, Louisiana, 1989, collection of G. G. Marten. Mexico: USNM 251674, 1 CV ♂, Lake Pátzcuaro, Michoacán, 19°30′N, 101°38′W, 17 Oct 1991, leg. A. Orbe-Mendoza and P. Aguilar. USNM 259699, 1 ♀, Cenote Viejo, Quintana Roo, Mexico, 21 Jul 1987, leg. E. Suárez-Morales. Guatemala: USNM 250931, 6 ♀♀ 4 ♂♂ 1 copepodid stage V (CV) ♀, all mounted on 2 slides, 16 Mar 1972, and 3 ♀♀ 1 ♂, all mounted on 3 slides, 19 Aug 1972, Lake Izabál, leg. L. G. Brinson, prep. det. H. C. Yeatman. Nicaragua: USNM 259614, 1 ♀ (dissected on slide), 1 ♂ 5 copepodids, Lake Nicaragua (Lake Cocibolca), Managua, 1991. USNM 259616, 6 ♀♀ 1 ♂ 57 copepodids, Lake Nicaragua, 1993. USNM 243696, 10 ♀♀, Lake Asososca, Managua, 22 Oct 1991. USNM 243700, 10 ♀♀ 10 ♂♂, Lake Las Canoas, 21 Jan 1993. USNM 243701, 8 ♀♀ 3 ♂♂, Lake Nicaragua, Sample 97-11, 13 Jun 1997. USNM 243707, 200+, Lake Nicaragua, Samples N97-09 and N97-11, 13 Jun 1997. USNM 243710, 100+, Lake Asososca, Managua, 22 Oct 1991. USNM 243713, 500+, Lake Managua, Point 7, 23 Mar 1995. USNM 243715, 100+, Lake Las Canoas, 21 Jan 1993. Legs. L. Moreno. Additional material deposited in the Plankton Collection, CIRA/UNAN. Cuba: 1 ♀, partly dissected on slide, Sabanilla Reservoir, 15 May 1965, collection of C. H. Fernando.

Supplementary description of female.—We describe certain morphological features of the adult female, to supplement previous redescriptions (Dussart 1985, Dahms & Fernando 1995a).

Medians (ranges, *n*) of lengths, excluding caudal setae, in mm: Canada: Ontario (USNM 79773), 1.41 (1.24–1.48, $n = 10$); Nova Scotia (USNM 251908), 1.43 (1.38–1.49, $n = 6$). U.S.A.: Lake Erie (USNM 62590), 1.23 (1.06–1.33, $n = 10$); Florida (USNM 78730), 1.27 (1.09–1.35; $n = 10$); North Carolina (USNM 216873), 1.31 (1.22–1.38, $n = 10$); Utah (USNM 235221), 1.17 (1.11–1.18, $n = 7$); Louisiana (Marten collection), 1.40 (1.26–1.53, $n = 10$); Texas (USNM 264309), 1.30 (1.28–1.36, $n = 10$). Mexico: Quintana Roo (USNM 259699), 1.08 ($n = 1$). Guatemala: Lake Izabál

(USNM 250931), 1.26 (1.23–1.40, n = 9). Nicaragua: Lake Nicaragua (Lake Cocibolca) (USNM 259614), 1.18 (n = 1); Lake Nicaragua (USNM 259616), 1.38 (1.26–1.45, n = 6); Lake Asososca (USNM 243696), 1.02 (0.96–1.15, n = 10); Lake Las Canoas (USNM 243700), 1.17 (1.09–1.31, n = 10).

Habitus (Fig. 1A) typically cyclopiform; occasional individuals with circular pits on prosomites. Pediger 5 (Fig. 1B–E) usually without ornament except normal hair-sensilla, except group of hairs on lateral surfaces in one female from Nicaragua. Genital double somite (Fig. 1B–D) with group of 6 tiny pores posterior to leg 6, pore pattern otherwise as in figures. Pore-canal usually single as in Fig. 1D, but sometimes appearing divided (Fig. 1F, G). Posterior pore-canal usually represented as stout and posteriorly directed, but strongly recurved in oblique view (in direction of arrows, Fig. 1G). Anal somite (Fig. 1H) with continuous row of spines along posterior margin; caudal ramus usually divergent in preserved specimens, with 4–5 irregular groups of hairs on medial surface.

Hyaline membrane of antennule terminal segment beginning at lateral seta, usually with several large notches (Fig. 2A). Specimen from Cuba with this condition exaggerated on one side, giving impression of single deep notch (Fig. 2B).

Antenna basis (Fig. 2C–F) in most populations with secondary curved row of small spines (Fig. 2E, arrow; Dahms & Fernando 1995a), row absent in some populations (Fig. 2C).

Maxilla (Fig. 2G) with group of tiny spines on frontal side.

Maxilliped (Fig. 2H, I) usually with more complex surface spine pattern than indicated by Dahms & Fernando (1995a).

Legs 1–4, caudal surfaces of coxa-bases ornamented as in Fig. 3A–D. Medial spine of leg 1 basipodite with slender spinules in North American populations (Fig. 3A), with more and stouter spinules in some southern populations, e.g., Cuba (Fig. 3E). Couplers (intercoxal sclerites) of legs 1–3 always with small submarginal spinules (Fig. 3F–H, J–L), number of spinules on leg 1 coupler varying from 1 to 5 in North American populations and from 7 to 10 on specimen from Cuba, with similar, but fewer spines on couplers of legs 2 and 3. These spines usually stout, but slightly longer and slimmer in specimens from Guatemala and Nicaragua. Two projections on margin of leg 4 coupler usually rounded (Fig. 3M), but sometimes acute and inward- or outward-directed (Fig. 3D, I). Both terminal spines of leg 4 endopodite 3 with spinulate margins, spinules of lateral terminal spine fewer and coarser than spinules of medial terminal spine in all specimens examined (Fig. 3N).

Discussion

Balcer et al. (1984), Coker (1943), Cole (1960), and Patalas (1986) traced the changing descriptions and taxonomy of *Mesocyclops edax*. These changes are a story of advances in understanding the taxonomy of the genus *Mesocyclops* and the morphologically similar genus *Thermocyclops* (see also comments by Dahms & Fernando 1995a, 1995b). In spite of much previous discussion, three points remain to be resolved.

The synonymy of Mesocyclops nicaraguensis *Herbst, 1960.*—The question of the possible synonymy of *M. nicaraguensis* Herbst, 1960, which was described from Lake Nicaragua, was first raised by Cole (1976). Yeatman, who determined Cole's Nicaraguan copepods, affirmed Cole's opinion (H. C. Yeatman, in litt. to JWR, 1991). Reid (1990) also proposed the synonymy. Absent formal examination, however, *M. nicaraguensis* has continued to be treated as a distinct taxon (e.g., Cisneros & Mangas 1991, Collado, 1984, Dussart & Fernando 1986). The type specimens of *M. nicaraguensis* cannot be located (H.-V. Herbst, in litt. to JWR, 1991), and there is no non-type material from the original collection

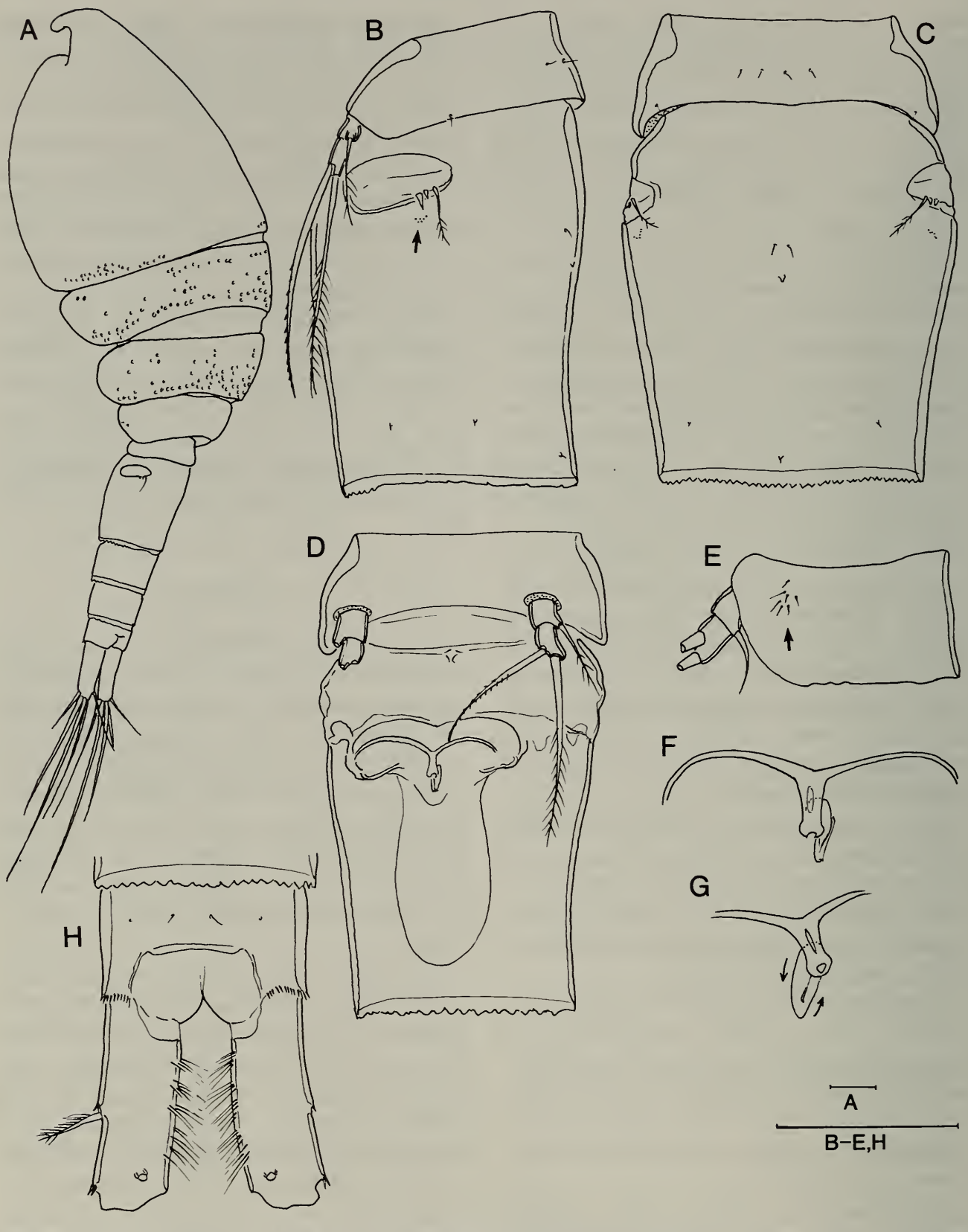

Fig. 1. *Mesocyclops edax,* female. A–C, F–H, specimens from North Carolina, U.S.A. (USNM 216873); D, Louisiana, U.S.A. (Marten Collection); E, Lake Nicaragua (USNM 259614). A, Habitus, lateral; B, Pediger 5 and genital double somite, left lateral; C, Pediger 5 and genital double somite, dorsal; D, Pediger 5 and genital double somite, ventral (leg 5 setae foreshortened); E, Pediger 5, left lateral; F, Copulatory pore and pore-canal, ventral, enlarged; G, Copulatory pore and pore-canal, ventral-oblique, enlarged; H, Anal somite and caudal rami, dorsal. Scales equal 100 μm.

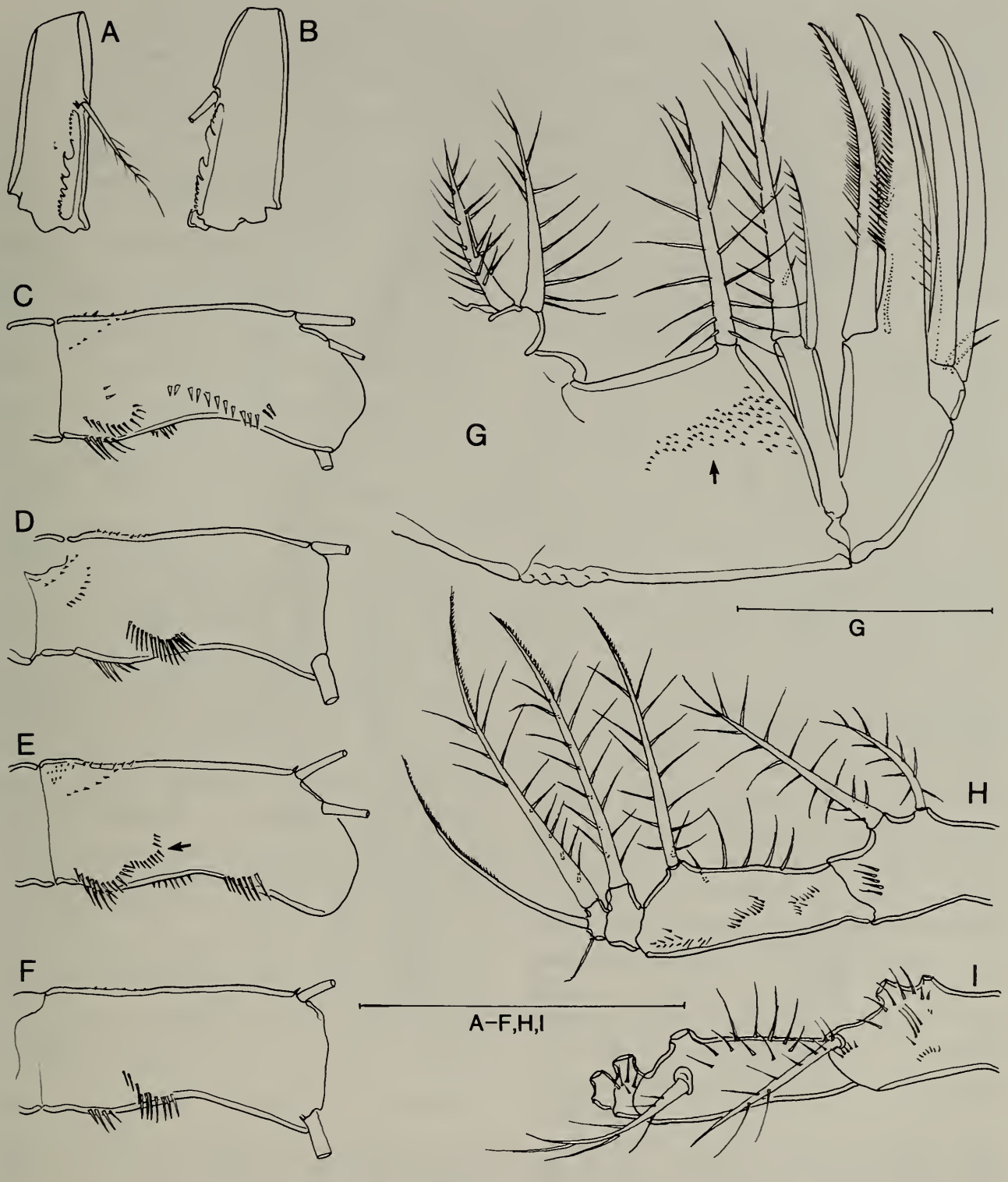

Fig. 2. *Mesocyclops edax,* female. A, C, D, G–I, specimens from North Carolina (USNM 216873); B, E, F, Specimen from Cuba (Fernando Collection). A, B, Antennule terminal segment; C, E, Antenna basis, caudal side; D, F, Antenna basis, frontal side; G, Maxilla, frontal side; H, I, Maxilliped. Scales equal 100 μm.

(G. Hartmann, in litt. to JWR, 1991). No material remains from Cole's (1976) study of Lake Nicaragua (H. C. Yeatman, in litt. to JWR, 1991).

There are a few differences between published descriptions of *M. edax* and *M. nicaraguensis.* The most obvious is the lengths of adult females, 0.83–1.1 mm for *M. edax* (Dahms & Fernando 1995a, Dussart 1985) and about 1.45 mm for *M. nicaraguensis* (Herbst 1960). This difference in lengths was the only discriminator used by Dussart (1987) and Petkovski (1986) in their keys to American *Mesocyclops.* How-

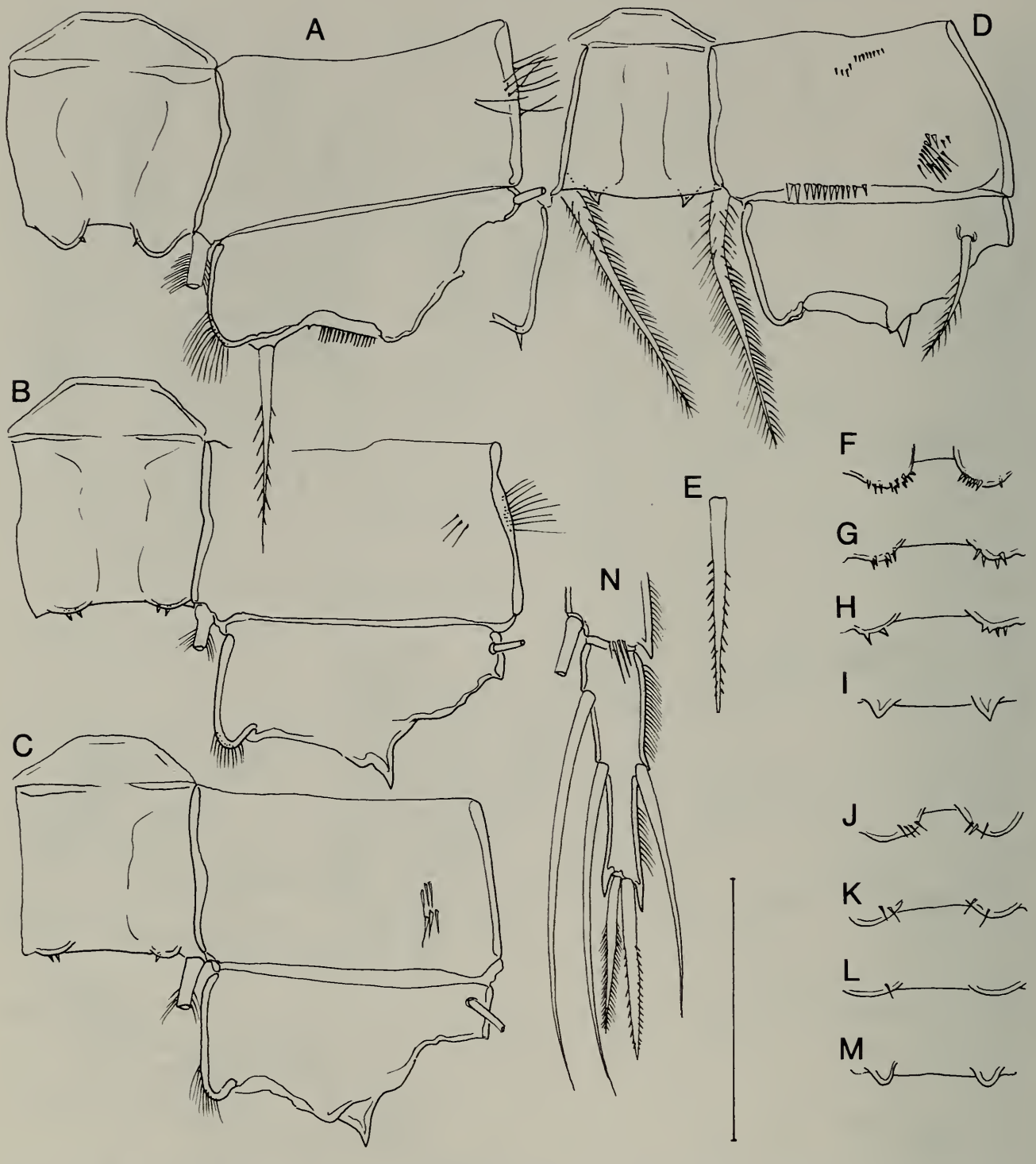

Fig. 3. *Mesocyclops edax,* female. A–D, N, specimens from North Carolina (USNM 216873); E–I, Cuba (Fernando Collection); J-M, Guatemala (USNM 250931). Scale equals 100 μm.

ever, we report populations of *M. edax* from Ontario, Nova Scotia, and Louisiana with individuals longer than 1.45 mm. Lengths of females from lakes in Nicaragua varied from 0.96 to 1.45 mm. There is then no meaningful difference in the lengths of northern and southern populations, nor is there any correlation between length and latitude.

The remaining apparent difference consists of the presence of submarginal spines on the leg 1 coupler in *M. edax,* while Herbst (1960: fig. 37) indicated no ornament on the leg 1 coupler in *M. nicaraguensis.* However, all specimens from Lake Nicaragua examined by us had such spines. A single female from Nicaragua bore small spines on the lateral surface of pediger 5

(Fig. 1E). The presence or absence of spines at this location is a much used character in the genus systematics. However, the facts that this condition is apparently extremely rare and found only in one Nicaraguan population, and that all females from Nicaragua were otherwise congruent in all respects with the diagnosis of *M. edax,* persuaded us to consider *M. nicaraguensis* synonymous with the former taxon.

Habitat as well as genetic factors may account for some variation. Barwick & Hudson (1985) reported that individuals of *M. edax* in the tailwater of a reservoir were small and the posterior edges of the urosomes were sculptured, in contrast to a "reservoir form" that averaged larger and had smooth urosomal edges. Specimens were, however, unavailable (P. L. Hudson, in litt. to JWR, 1998). Wyngaard et al. (1985) noted differences in body size, clutch size, and egg size among wild populations from Michigan and Florida.

The taxon Cyclops tenuissimus *(Herrick, 1883).*—Cole (1960) suggested that *Cyclops tenuissimus,* described by Herrick (1883) from Kentucky, U.S.A., is a senior synonym of *M. edax.* Cole pointed out that the combination of several characters, the relationships of the lengths of the leg 5 terminal seta and subterminal spine, the antennular hyaline membrane with several small notches, and the caudal rami hairs possessed by *C. tenuissimus* matches only *M. edax* among North American cyclopoids. However, Herrick showed the genital segment of *C. tenuissimus* as very slender and the seminal receptacle with narrow lateral and posterior extensions, and in his text described (and named) this species as "the most slender cyclops known to me". Cole's argument might easily be accepted if not for the contradictions between Herrick's description and the relative robustness of *M. edax* and the broad lateral and posterior expansions of its seminal receptacle. Since Herrick's description matches no presently known American cyclopoid species in all respects, in our opinion the identity of Herrick's specimens remains in question.

The western and southern distribution of M. edax.—The published records from Pacific drainage basins in the U.S.A. and Canada are few and relatively recent. Several were confirmed by material made available for this report, and we consider all of them entirely reliable. Simenstad & Cordell (1985) listed *M. edax* from the Columbia River basin in Washington State. The previously unpublished record herein from Lake Union, Washington, also comes from the Columbia River basin. The few records from the Colorado River basin include those of Soto & Hurlbert (1991a, 1991b) from California, and of Maddux et al. (1987) and Sollberger & Paulson (1992) from the Colorado River in Arizona and Nevada. The records reported herein from San Diego and Fresno, California are new. In western Canada, *M. edax* was recently reported from British Columbia (Chengalath & Shih 1994, Shih & Chengalath 1994).

Only recent reports of *M. edax* from Mexico, Central America, and the Antilles are reliable. As noted by Cole (1960), prior to and even following the revision of Coker (1943) which established the distinction between *M. edax* and populations in the Americas referred to as *M. leuckarti, M. edax* was likely to be reported as *M. leuckarti* (e.g., Comita 1950). In the Americas, records of *M. leuckarti* may refer to other members of the *leuckarti*-group, such as *M. americanus* Dussart, 1985, *M. aspericornis* (Daday, 1906), or *M. ruttneri* Kiefer, 1981, or even to any of several species of *Thermocyclops* now known to be present in the region (Dussart 1985, Dussart & Fernando 1990, Reid 1993, Reid & Reed 1994). Cole (1960) pointed out inconsistencies in Marsh's (1910) description of *M. leuckarti* which apparently led Marsh to synonymize *M. edax* with the former species. Examples of Marsh's confusion can be found among the slide-mounted specimens labeled "*M. leuckarti*" in the Marsh Collection at the

National Museum of Natural History. Among these specimens one of us (JWR) has identified *M. longisetus* (Thiébaud, 1912), *M. reidae* Petkovski, 1986, *M. venezolanus* Dussart, 1987, and *Thermocyclops decipiens* Kiefer, 1929b, but neither *M. leuckarti* nor *M. edax.* The extensive Marsh Collection contains no unequivocal specimen of *M. edax* from any locality south of Texas. Pearse's (1921) record of *M. leuckarti* var. *edax* from Lake Valencia, Venezuela, may refer to *M. brasilianus* Kiefer, 1933, as suggested by Infante et al. (1979), or to some other congener with haired caudal rami, such as *M. aspericornis* which also occurs in Lake Valencia (Reid & Saunders 1986). Pearse's (1915) record of *M. leuckarti* var. *edax* from Colombia is similarly suspect.

Additional problems are the sparsity of general collections of plankton from Central America and the Antilles, and the presence of *M. edax* and *M. leuckarti,* but not other congeners, in the widely used key of Yeatman (1959). Before publication of the keys to American *Mesocyclops* by Petkovski (1986) and Dussart (1987) and a local checklist by Reid (1990), any of the many congeners in the region was likely to be identified as one of those two species. Similar doubts as to the validity of Central American records were implied in the summary by Collado, Fernando, & Sephton (1984) of the distribution of zooplankters from this area, since those authors included no records of *M. edax* other than those from Cuba by Smith & Fernando (1978, 1980).

Smith & Fernando's record from Cuba is the only report of *M. edax* from the Antilles, and is supported by preserved material.

Most of the few Mexican and Central American records of *M. edax* can be likewise verified. Coker (1943) and Osorio-Tafall (1944) reported *M. edax* from Lake Pátzcuaro, Mexico. Copepodids of *Mesocyclops,* including one stage V copepodid referable to *M. edax* from Lake Pátzcuaro examined for this report substantiate their records. *Mesocyclops edax* was reported from the Yucatán Peninsula (and specimens archived) by Suárez-Morales et al. (1996). The reports by Brinson & Nordlie (1975) and Deevey et al. (1980) from eight or more lakes including Lake Izabál in the Guatemalan lake district were substantiated by the specimens furnished by H. C. Yeatman.

The scarcity of reports of *M. edax* south of the U.S.A. may correctly reflect its distribution. General collections, mainly from shallow waterbodies in Costa Rica (Collado & Fernando 1984) and Honduras (Marten et al. 1994) failed to record this species. The presence of *M. edax* in several large Central American lakes and its apparent absence from smaller waterbodies might imply some direct temperature effect. On the other hand, it was collected from Laguna Sabanilla near Havana, Cuba, which is shallow (maximum depth 1.3 m) and near sea level (Straskraba et al. 1969). Some of the Guatemalan lakes are also shallow, such as Petenxil (4 m maximum; Deevey et al. 1980). Better adapted neotropical cyclopoids may outcompete *M. edax* in most conditions. One candidate might be *Thermocyclops decipiens,* which is a pantropical facultatively omnivorous plankter that is frequently successful in the mesotrophic to eutrophic conditions in which *M. edax* also thrives (Reid 1989). It is usual for *M. edax* and the much smaller *Thermocyclops inversus* Kiefer, 1936 to co-occur (Coker 1943, Cole 1976, Deevey et al. 1980, Osorio-Tafall 1944, and our samples from Nicaragua). In Guatemala, *T. decipiens* (reported by Deevey et al. [1980] as *Mesocyclops hyalinus* [Rehberg, 1880], a synonym) occurred with *M. edax* in only one lake. *Thermocyclops decipiens* was also numerous in the sample from Laguna Sabanilla examined for this report. *Thermocyclops decipiens* ranges from 0.75–0.99 mm in length, thus approaching the length of *M. edax.* It is common in the Antilles including Cuba and in Central America (Reid 1985, 1989), but does not extend northwards past southern Mexico (Suárez-Morales & Reid 1998).

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